Cryptoendolithic communities from hot and cold deserts: Speculation on microbial colonization and succession

J. R. VESTAL*

*Department of Biological Sciences,
University of Cincinnati, Cincinnati, Ohio 45221−0006, USA*

SUMMARY

1 The cryptoendolithic microbial community is a complete ecosystem containing primary producers and consumer/decomposers located within the pores of certain types of rocks. It has no predators.

2 This unique habitat provides enough protection for microbes to survive a physical environment characterized by extreme temperatures, aridity, low light and limited space.

3 As conditions for metabolic activity are so limited in both frequency and duration, determining colonization and succession events in this environment is very difficult.

4 Two types of community are recognized: one dominated by lichens and the other by cyanobacteria. The distribution of the communities appears to be related to water availability, the presence of iron oxide and rock strength.

5 It is postulated that within these endolithic communities succession may only occur in the decomposer microbiota, and that the plant community constitutes a climax at establishment.

INTRODUCTION

Biotic succession at the microbial level is different from the ecologist's normal expectations formed by studies of plant succession. The basic processes are similar: initial colonization by pioneer species, followed by successional sequences during which species changes occur due to competition and/or changes in the physical and chemical environment. The differences are in the size of the organisms, the length of time for successional events and the relative instability of microbial communities in relation to environmental change. For example, a complete successional sequence of microbes could occur in a 1 ml sample of milk in a few hours.

In this review, a unique microbial ecosystem will be discussed. It is one which

---

* J. R. Vestal died August 1992.

occurs in extreme hot and cold deserts and is limited by space, light, moisture, temperature and the chemical milieu. These limitations are so severe that growth is extremely slow and therefore succession must be considered on a time-scale of hundreds to thousands of years. The numerous studies on this microbial ecosystem have mainly involved characterization of the species and the effects of environmental variables on growth and metabolism. It has been difficult actually to study succession due to the slow turnover of the microbial community, but studies are underway to attempt to look at changes in the activity, biomass, metabolic status and community structure in this microbial ecosystem. In order to properly discuss the successional events, the system will be described in terms of its physical and chemical features, and how these affect growth and metabolism. Possible routes for colonization and succession will then be discussed.

Endolithic (within rocks) microbial communities exist inside hard substrata, such as sandstones, quartz, limestones, shale and coal. These endoliths can be subdivided into cryptoendoliths which usually live within the pore spaces of rock, (usually sandstones), chasmoendoliths that inhabit the fissures or cracks of a rock and euendoliths which actively penetrate calcareous substrata (Golubic *et al.* 1981).

The particular microbiota discussed here are considered to be crytoendolithic because the organisms inhabit the interstices of sandstones. The physical and chemical environments of cryptoendoliths are important in allowing as well as controlling microbial growth. In the cryptoendolithic microbiota discussed here, lichens, containing photobionts, and cyanobacteria are the dominant primary producers.

THE POLAR CRYPTOENDOLITHIC ENVIRONMENT

In 1976, Friedmann & Ocampo-Friedmann first described a cyanobacteria-dominated microbial cryptoendolithic community in the Ross Desert (Dry Valley) region of Antarctica at about 78°S. Some sandstones were found to contain a lichen-dominated microbial community characterized by the lichens *Buellia* or *Lecidea* (Friedmann 1982; Hale 1987) while others were dominated by cyanobacteria (Friedmann *et al.* 1989). Examples of cyanobacterial and lichen cryptoendolithic communities are shown in Fig. 1. The lichen-dominated community (Fig. 1A) is characterized by a black layer of lichen 1–3 mm inside the rock. This layer overlays a light coloured layer containing filamentous fungi, yeasts and bacteria. Often, but not always, there is a lower green layer characterized by green algae (Tschermak-Woess & Friedmann 1984). In the cryptoendolithic cyanobacteria community (Fig. 1B), there is only one visibly dark layer under the surface containing the cyanobacteria. There are heterotrophic eubacteria also associated with this layer, but invisible to the naked eye.

This unique ecosystem has been extensively studied and members of the community identified. Other components of the microbiota include a new green algal species, *Hemichloris antarctica* (Tschermak-Woess & Friedmann 1984), yeasts
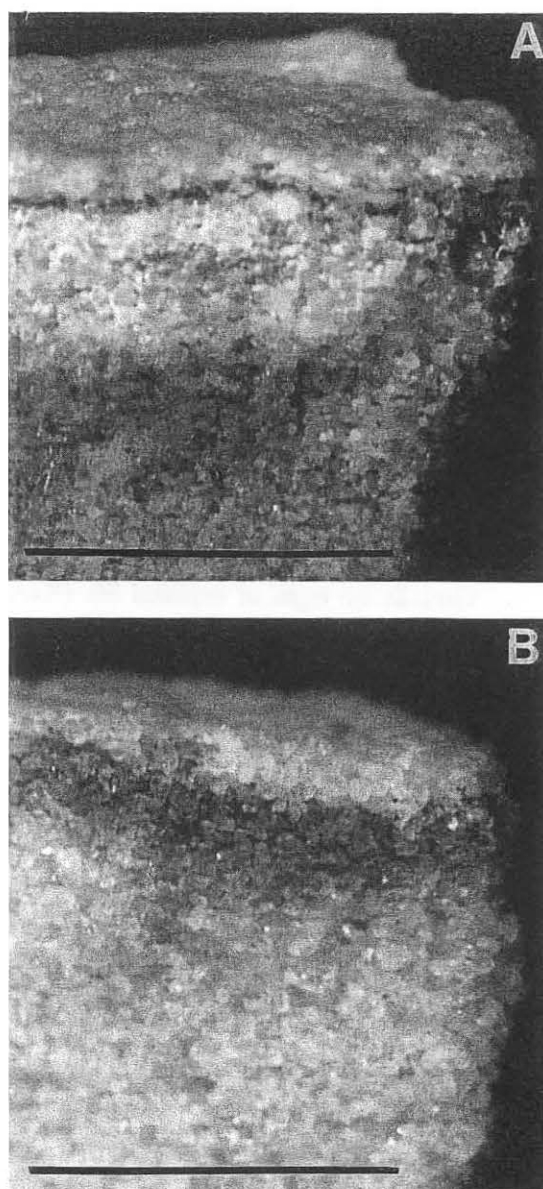
FIG. 1. (A) Cross-section of the cryptoendolithic lichen microbiota from Antarctica. The top dark band is lichen, followed by a white band containing filamentous fungi and other heterotrophic microbes. The grey region below the light band is stained by orange-coloured iron oxides. (B) Cross-section of the cryptoendolithic cyanobacterial microbiota from Antarctica. The top dark band contains the cyanobacteria. Below that band is the rock interior which is not stained by iron oxides. Bar markers are 1 cm.

(Vishniac 1985a), filamentous fungi (Friedmann 1982) and bacteria (Siebert & Hirsch 1988). A new species of bacteria from the Antarctic cryptoendolithic microbiota was found using 5S rRNA sequence analysis (Colwell *et al.* 1989). A detailed description of existing Antarctic cyanobacteria was recently published (Friedmann *et al.* 1989).

Since the discovery of these primitive ecosystems, many studies have focused on this habitat, including geochemistry (Weed 1985; Friedmann & Weed 1987; Johnston & Vestal 1989a, b), nanoclimate (McKay & Friedmann 1985; Friedmann *et al.* 1987), taxonomy (Friedmann 1982; Friedmann *et al.* 1989), nitrogen economy (Friedmann & Kibler 1980), biomass (Tuovila & LaRock 1987; Vestal 1988a), unique freezing properties of the membranes of the lichen-dominated community (Finegold *et al.* 1990) and physiology and carbon metabolism (Vestal 1988b). The functional interactions of these microbes living in such an extreme environment have also been mathematically modelled (Nienow *et al.* 1988a, b). In addition, microbial life in the extremes of polar environments has been recently reviewed (Longton 1988; Vincent 1988; Vincent & Ellis-Evans 1989; Wynn-Williams 1990).

The climate of the Ross Desert, Antarctica, is cold and dry, and there are virtually no signs of exposed life (Kappen *et al.* 1981). In the region where the Beacon sandstone is found colonized with cryptoendolithic lichens or cyanobacteria, the air temperature is consistently below freezing, the mean annual air temperature being −22°C. During the warmest months of the year, December and January, the mean air temperature is *c.* −7°C (Friedmann *et al.* 1987). There is little snow and much of what falls sublimes or is blown away by the frequent katabatic winds. Occasionally, the rocks are warmed by the sun and any remaining snow melts into the pores and serves as the source of water for the microbiota (Friedmann 1978).

The physical environment

The physical factors that impede exposed or epilithic life on the surface of soils or rocks are listed in Table 1. These factors are buffered if the organisms are

TABLE 1. Physical factors which affect the metabolic activity of the Antarctic microbiota, and the advantages of the cryptoendolithic habitat

Factor	Cause	Advantages of the cryptoendolithic habitat
1. Low moisture	Little snow, air humidity <50%	Rock matrix holds moisture for days after snowmelt
2. Low temperature	Air <0°C with frequent fluctuations	Direct solar heating warms rocks and thermal inertia dampens temperature variation
3. Variable radiation	High UV flux and intense visible light	Rock attenuates all radiation particularly UV
4. High wind velocity	Abrasion by strong katabatic winds	Protection by the rock

endolithic and they may operate together to influence the cryptoendolithic nature of these organisms. Most importantly, the rock provides a matrix for holding moisture, generated during the occasional summer snowfalls, to counteract loss to the dry environment (Friedmann *et al.* 1987). After a snowmelt, the moisture level in the rock can remain high (*c.* 80−100% relative humidity, RH) for up to 10−14 days while the outside air RH remains quite low (*c.* 10−30%) (Friedmann *et al.* 1987). Additionally, direct solar heating of the rock can raise the inside temperatures to 5−10°C and the rock provides a relatively thermally stable environment due to its thermal inertia (McKay & Friedmann 1985). Light is another important factor which affects life in the cryptoendolithic community. On the rock surface, the light intensity varies diurnally from *c.* 50−1800 μmol m^{-2} s^{-1} (Friedmann *et al.* 1987). Nienow *et al.* (1988b) showed that light intensity was attenuated about an order of magnitude per millimetre depth within the porous sandstone. Thus, light intensities of 1·0−0·1 μmol m^{-2} s^{-1} would be found in the lower portions of the biotic zone, which is 1−5 mm inside the rock matrix. The rock also provides a mechanical shield against wind abrasion from the strong katabatic winds coming from the polar plateau. Even though the cryptoendolithic microbiota has adapted to living in this 'sheltered' niche, the microbial community is still living under the environmental stresses of low temperature, low moisture, low light intensity and little space for growth throughout most of its existence.

The chemical environment

Chemical factors which affect the Antarctic cryptoendolithic lichen and cyanobacterial microbiota mainly involve the availability of essential elements and pH. In a comparative study of the chemical species in lichen and cyanobacterial communities, Johnston & Vestal (1989a) showed that the chemical environment of the lichen community had higher amounts of the oxides of iron, aluminium and manganese than the cyanobacterial community. In the cyanobacterial community, the dominant inorganic species were water-soluble calcium and magnesium. Potassium and phosphate were readily available in high (0·2−0·4 mg g^{-1} rock) amounts in both microbiota. Chloride and sulphate were found in small (50 and 4 μM, respectively) concentrations in the biotic zone of lichen-dominated rocks (C. G. Johnston, pers. comm.) suggesting that the microbiota was not under an abnormally high osmotic stress when the rock interstices were saturated with water. However, as the rock dries, solutes will become more concentrated and could exert a transient osmotic stress, which could affect microbial metabolism for a short time. Water-soluble silica was much more prevalent in the cyanobacterial rocks compared with the lichen-containing rocks. The redox potential (pE) of the cyanobacterial community was about four times lower than in the lichen community (*c.* 8·2). The pH ranged from 5 to 6 in the lichen community and between 8 and 9 in the cyanobacterial community. These differences in pH indicate that the lichen community probably produces acidic organic compounds to maintain the low pH. Johnston & Vestal (1989b) have found rather high amounts of oxalate in water

extracts of the lichen community, but much lower amounts in the cyanobacterial community. The cyanobacterial community has a higher pH, probably due to the production of organic amines. Aquatic cyanobacteria commonly prefer a pH in the range of 7–9 (Rippka *et al.* 1981).

Cryptoendolithic lichen community physiology

It was recently shown (Vestal 1988b) that the community photosynthetic metabolism was psychrophilic (Morita 1975); that is, it has a photosynthetic optimum below 20°C and some metabolic activity at 0°C or less. Photosynthetically driven CO_2 fixation was measurable after 12 hours at −8°C and after 4 hours at −5°C. At 0°C, photosynthetic activity was relatively high but only *c.* 40–50% of the optimum rate, which was at 15°C (Vestal 1988b). The period above 0°C for a typical cryptoendolithic community is less than 300 hours per year, with 50–100 hours being more typical (Nienow *et al.* 1988a; Vestal 1989). This suggests that the community rarely has temperatures in its optimum metabolic range of 10–15°C. The community is therefore living under suboptimal temperature conditions, which may place it in a constant state of metabolic stress.

Biomass of the cryptoendolithic lichen community was measured indirectly by lipid phosphate (Vestal 1988a) and adenosine triphosphate (Tuovila & LaRock 1987). Both methods showed *c.* $2 \cdot 54 \, \mathrm{g \, m^{-2}}$ of carbon as viable biomass in the cryptoendolithic community. This compares with $1600 \, \mathrm{g \, m^{-2}}$ for a temperate grassland to $45\,000 \, \mathrm{g \, m^{-2}}$ for a tropical rain forest (Table 2). Using photosynthetic rate measurements (Vestal 1988b), biomass estimates, and assumptions about the length of time temperatures were above −5°C, light intensity was above $10 \, \mathrm{\mu mol \, m^{-2} \, s^{-1}}$ and moisture was present within the interstices of the rock, it was calculated that the primary production was between $0 \cdot 11$ and $4 \cdot 4 \, \mathrm{mg}$ carbon

TABLE 2. Comparison of biomass, production and carbon turnover time of the Antarctic cryptoendolithic microbial ecosystem to other ecosystems around the globe (after Vestal 1989)*

Ecosystem	Biomass (g carbon m^{-2})		Production (g carbon m^{-2} year^{-1})	Turnover (years)
Ross Desert,	2·54	(min.)	0·000108	23 520
Antarctica	2·54	(max.)	0·00441	576
Tropical rain forest	45 000		2200	20·5
Temperate evergreen	35 000		1300	26·9
Temperate deciduous	30 000		1200	25
Temperate grassland	1600		600	2·7
Tundra and Alpine	600		140	4·3
Swamp and marsh	15 000		2000	7·5
Agricultural land	1000		650	1·5
Open ocean	3		125	0·024
Continental shelf	10		360	0·027
Estuaries	1000		1500	0·7

* All non-Antarctic data are from Whittaker (1975) and Antarctic data are from Vestal (1989).

m^{-2} year^{-1} and the carbon turnover was 576–23 500 years (Vestal 1989) (Table 2). This places this cryptoendolithic microbial community as having the lowest primary production and the longest carbon turnover of any ecosystem on Earth (Table 2). The turnover time estimates were based on laboratory and field measurements and many assumptions. Consequently, they must be regarded with caution and as illustrative of the slow growth of these rock communities under natural physical and chemical conditions. It could be that exfoliation of the rock surface (see below) may play an important role in microbial colonization and succession, which could affect the carbon turnover times, making them shorter than the above calculations. It is not clear how such turnover times could be measured directly in the field.

Over long periods of time, the microbiota appears to weaken the structure of the rock by some sort of dissolution. This allows rather large (c. 2–5 cm diameter) pieces of rock surface to loosen and eventually be removed by the wind. When this exfoliation occurs, the biotic zone in the rock is exposed, revealing a mosaic of lightly coloured areas leached of iron oxides (Fig. 2). This exfoliative pattern is a common characteristic of lichen-colonized rocks.

In most cyanobacterial rocks, there are usually no iron oxide deposits. However, it has been observed that the rocks may exfoliate more rapidly than lichenized

FIG. 2. A large plate of sandstone containing the cryptoendolithic lichen microbiota from the Ross Desert, Antarctica. Note the mosaic pattern produced by rock exfoliation on the surface of the rock. Scale is noted by the head of the geology pick at the bottom of the picture.

rocks, possibly due to the high pH of these communities, which may cause more rapid dissolution of the silica matrix. The cyanobacteria rocks are quite friable and lack iron oxide, so that exfoliation may occur more at a grain-by-grain level, rather than in large pieces.

In addition to the Antarctic cryptoendolithic communities, there has been a report of cryptoendolithic microbial communities living in sandstones in the high Arctic, at *c*. 80°N (Eichler 1981). It was indicated that there was an exfoliative pattern of weathering of the sandstone surfaces similar to the patterns observed in Antarctic sandstones. Subsequent observations by E. I. Friedmann (pers. comm.) did reveal the presence of the lichenized microbiota in these Arctic rocks, but no detailed studies of these Arctic cryptoendoliths have been made.

HOT DESERT CRYPTOENDOLITHS

Cryptoendolithic microbial communities can also be found in hot deserts such as the Negev, Sinai and in the south-west of the United States (Friedmann & Ocampo-Friedmann 1984). These communities, which are exclusively cyanobacterial, also inhabit the pore spaces of sandstones. It appears that they have adapted to porous sandstones for some of the same reasons as the cold desert cryptoendoliths. Confinement within a fixed space inside the sandstone offers more chances for moisture for growth, and some transient protection from the extremely high temperatures on the surface of the rocks during the daytime. Light availability, which is similar to that in the Antarctic sandstones, restricts the photobionts to the top 1–5 mm inside the rocks. The temperature regime is different in that the rock can cool to 27–28°C during the night and then rise to 46–48°C during the day (Friedmann 1980). It is thought that the source of water for hot desert cryptoendoliths is occasional rain and dew condensation on the rocks at night. This at least increases the relative humidity inside the rocks so that during the morning when light is available, metabolic activity can occur for a short time before the water vapour is evaporated by increasing temperatures. When this occurs, the cells become desiccated and activity ceases until the next diurnal cycle.

The hot desert rocks have not been studied as extensively with regard to their physiology and metabolism, but the effects of water stress on hot desert cyanobacterial cultures have been examined (Potts & Friedmann 1981). In that study, it was demonstrated that a desert *Chroococcidiopsis* species could survive low water potentials (*c*. −20 000 kPa) for a short time (i.e. 24 hours), but was metabolically inert after 72 hours at *c*. −7000 kPa. A marine *Chroococcus* species, however, could tolerate low water potential for at least 72 hours. The nitrogen regimes of cold and hot desert cryptoendoliths have also been studied (Friedmann & Kibler 1980). It appears that the source of combined nitrogen in hot desert cryptoendoliths is the same as for the cold desert, that is, from atmospheric precipitation of nitrates and ammonia. Nitrogen fixation was extremely rare in both hot and cold desert communities.

COLONIZATION AND SUCCESSION
IN CRYPTOENDOLITHIC COMMUNITIES

Owing to the limiting environmental parameters just described, the processes of colonization and succession in cryptoendolithic communities are enigmatic. Some speculation is possible. Friedmann & Weed (1987) have shown that in the Antarctic, the Ross Desert sandstone containing the cryptoendolithic microbiota are from 70 000 years to 4 million years old. These sandstones are subject to katabatic winds as well as daily freeze/thaw cycles in the summer, and it seems reasonable to assume that at some point cracks developed either on the surface of the rock, through the rock or around the edges (see Fig. 2). Epilithic (attached surface growing) lichen species from the warmer protected areas in the Ross Desert as well as from the nearby coastal regions of McMurdo Sound have been described (Hale 1987) and are apparently the same as the species found within the rocks. It therefore seems plausible that, over geologic time, some of the lichen phyco- and mycobionts could have become windborne. By chance, they could have become lodged within a crack in the sandstone, and thus were able to grow laterally into the interstices of the rock, 'escaping' to a place where there was space, wind protection, periods of water availability, light and relatively mild temperatures. Lichens are commonly the first macroscopic colonizers on cooled volcanic lava flows (Alexander 1971; del Moral 1993) and survive easily in extremely cold and dry climates (Kappen 1973). As the endolithic lichens grew vegetatively they would completely inhabit the zone a few millimetres below the surface of the rock. Lichen acids as well as fungally produced short chain organic acids, such as oxalate, could be produced and would mobilize the iron oxide precipitates and create the lightly coloured (non-iron stained) biotic zones one observes (Fig. 1a). As growth occurs over time, the microbiota could 'loosen' the cement which holds the sandgrains together and produce the exfoliation pattern characteristic of these lichenized rocks (Fig. 2; Friedmann 1982). The lichen microbiota attached to the exfoliated rock could then serve as potential colonizers for other non-colonized rocks. If the rocks were colonized by aerial transport of lichens in this way, succession in the traditional sense has not taken place. There were no competitors so that the community established was in a 'climax' condition from the beginning. It is hard to conceive of a situation where this community could be replaced by one more suitable to the rock environment. It seems reasonable also to assume that the cyanobacteria could not easily compete with an established lichen community, and vice versa, due to the quite different pH characteristics of each community/rock matrix (Johnston & Vestal 1989b).

The pattern of Antarctic cyanobacterial colonization and succession could have been similar to that of the lichen-colonized rocks in the Ross Desert. The major difference between the two is that cyanobacterial communities are generally associated with rocks that do not contain iron oxide stains, and are in locations which are wetter than lichen cryptoendolithic communities. These occur where

windblown snow would accumulate (e.g. cracks, protected ledges, etc.) and provide increased water resources within the rocks. Also, these rocks are generally more protected from direct winds which would blow the snow away. At Battleship Promontory, Ross Desert, cyanobacterial communities are frequently found at the base of sandstone outcrops along the edges of a dolerite pavement. The dolerite has a low albedo, which causes snow to melt rapidly and infiltrate the nearby sandstones. These rocks then become saturated with water, which seems to remain for longer periods than in rocks a few metres higher and more subject to the full force of the wind. These factors may all contribute to the development of a cyanobacterial- rather than a lichen-dominated community.

It can be speculated that similar mechanisms of colonization and succession could account for the presence of cyanobacteria in hot desert rocks.

The only successional events which seem possible in the cryptoendolithic microbiota would have been among the primary consumers/decomposers. These heterotrophic microbes, primarily bacteria, fungi and yeasts, probably arrived as airborne contaminants of snow or attached to dust particles. They would live off the organic excretion products from the lichen or cyanobacteria, as well as from dead cells and their own endogenous reserves. These microbes may have undergone metabolic competition sequences in order to establish a 'climax' decomposer community.

Since cryptoendolithic communities in Antarctica are living under such extreme conditions and have such short metabolically active periods each year (*c.* 50–100 hours of $>-5°C$, light and moisture) (Nienow *et al.* 1988a; Vestal 1989), their growth rates are extremely slow and generation times long. They may not even grow in the sense of increasing biomass, because of space limitations within the rock; they may just be carrying out minimal maintenance metabolism. In order to study succession in such slowly growing communities, long periods of time would be required. Some initial experiments have been set up by the author in the Ross Desert whereby various nutrients and inhibitors have been periodically added to the rock surfaces to percolate into the biotic zones. These chemical treatments include: (a) nitrate, ammonia and phosphate; (b) trace amounts of vitamins and other co-factors; (c) addition of the prokaryotic inhibitors penicillin and strepto-mycin; (d) addition of the eukaryotic inhibitor cycloheximide; and (e) glucose and acetate. These aqueous solutions have been added two to three times per season for four years (1983/84–1986/87), and it is anticipated that this will be repeated again in the near future. Inverted glass jars were attached to rocks to increase their temperature and thus allow greater metabolism than under ambient conditions. The jars were not completely sealed against the rock surface so that snow could still accumulate as a source of water for the rock microbiota. At some point in the future, the experimental rocks and their controls will be collected and the microbial activity, biomass, metabolic status and community structure will be determined using sensitive lipid analysis techniques (White 1983; Vestal & White 1989). The biochemical differences (if any) will be measured as an assay of microbial community change in response to these allogenic processes. At that

time, there may be more information from which actual successional events may be detectable, and the development of these communities can then be more objectively defined.

ACKNOWLEDGMENTS

REFERENCES

Alexander, M. (1971). *Microbial Ecology*. John Wiley and Sons, Inc., New York.

Colwell, R.R., MacDonell, M.T. & Swartz, D. (1989). Identification of an Antarctic endolithic micro-organism by 5S rRNA sequence analysis. *Systematic and Applied Microbiology*. **11**, 182–6.

del Moral, R. (1993). Mechanisms of primary succession on volcanoes: A view from Mount St Helens. *Primary Succession on Land* (Ed. by J. Miles & D.W.H. Walton), pp. 79–100. Blackwell Scientific Publications, Oxford.

Eichler, H. (1981). Small scale features of high arctic weathering in the Oobloyah Bay region, northern Ellesmere Island, N.W.T., Canada — Genesis and processes. *Heidelberger Geographische Arbeiten*, **69**, 465–85.

Finegold, L.X., Singer, M.A., Federle, T.W. & Vestal, J.R. (1990). Composition and thermal properties of membrane lipids in cryptoendolithic lichen microbiota from Antarctica. *Applied and Environmental Microbiology*, **56**, 1191–4.

Friedmann, E.I. (1978). Melting snow in the dry valleys is a source of water for endolithic microorganisms. *Antarctic Journal of the United States*, **13**, 162–3.

Friedmann, E.I. (1980). Endolithic microbial life in hot and cold deserts. *Origins of Life*, **10**, 223–35.

Friedmann, E.I. (1982). Endolithic microorganisms in the Antarctic cold desert. *Science*, **215**, 1045–53.

Friedmann, E.I. & Kibler, A.P. (1980). Nitrogen economy of endolithic microbial communities in hot and cold deserts. *Microbial Ecology*, **6**, 95–108.

Friedmann, E.I. & Ocampo-Friedmann, R. (1976). Endolithic blue-green algae in the Dry Valleys: Primary producers in the Antarctic desert ecosystems. *Science*, **193**, 1247–9.

Friedmann, E.I. & Ocampo-Friedmann, R. (1984). Endolithic microorganisms in extreme dry environments: Analysis of a lithobiontic microbial habitat. *Current Perspectives on Microbial Ecology* (Ed. by M.J. Klug & C.A. Reddy), pp. 177–185. American Society for Microbiology, Washington.

Friedmann, E.I. & Weed, R. (1987). Microbial trace-fossil formation, biogenous and abiotic weathering in the Antarctic cold desert. *Science*, **236**, 703–5.

Friedmann, E.I., McKay, C.P. & Nienow, J.A. (1987). The cryptoendolithic microbial environment in the Ross Desert, Antarctica: Satellite transmitted continuous nanoclimate data, 1984–1986. *Polar Biology*, **7**, 273–87.

Friedmann, E.I., Hua, M.S. & Ocampo-Friedmann, R. (1989). Cryptoendolithic lichen and cyano-bacterial communities of the Ross Desert, Antarctica. *Polarforschung*, **58**, 251–60.

Golubic, S., Friedmann, I. & Schneider, J. (1981). The lithobiontic ecological niche, with special reference to microorganisms. *Journal of Sedimentary Petrology*, **51**, 475–8.

Hale, M.E. Jr (1987). Epilithic lichens in the Beacon sandstone formation, Victoria Land, Antarctica. *Lichenologist*, **19**, 269–87.

Johnston, C.G. & Vestal, J.R. (1989a). Distribution of inorganic species in two Antarctic cryptoendolithic microbial communities. *Geomicrobioloy Journal*, **7**, 137–53.

Johnston, C.G. & Vestal, J.R. (1989b). The inorganic environment of two Antarctic cryptoendolithic microbial communities. *Abstracts Annual Meeting of the American Society for Microbiology*, **89**, 231.

Kappen, L. (1973). Response to extreme environments. *The Lichens*. (Ed. by V. Ahamdjian & M.E. Hale), pp. 310–80. Academic Press, New York.

Kappen, L., Friedmannn, E.I. & Garty, J. (1981). Ecophysiology of lichens in the Dry Valleys of southern Victoria Land, Antarctica: 1. Microclimate of the cryptoendolithic lichen habitat. *Flora*, **171**, 216–35.

Longton, R.E. (1988). *Biology of Polar Bryophytes and Lichens*. Cambridge University Press, Cambridge.

McKay, C.P. & Friedmann, E.D. (1985). The cryptoendolithic microbial environment in the Antarctic cold desert: Temperature variations in nature. *Polar Biology*, **4**, 19–25.

Morita, R.Y. (1978). Psychrophilic bacteria. *Bacteriological Reviews*, **39**, 144–67.

Nienow, J.A., McKay, C.P. & Friedmann, E.I. (1988a). The cryptoendolithic microbial environment in the Ross Desert of Antarctica: mathematical models of the thermal regime. *Microbial Ecology*, **16**, 253–70.

Nienow, J.A., McKay, C.P. & Friedmann, E.I. (1988b). The cryptoendolithic microbial environment in the Ross Desert of Antarctica: light in the photosynthetically active region. *Microbial Ecology*, **16**, 271–89.

Potts, M. & Friedmann, E.I. (1981). Effects of water stress on cryptoendolithic cyanobacteria from hot desert rocks. *Archives of Microbiology*, **130**, 267–71.

Rippka, R., Waterbury, J.B. & Stanier, R.Y. (1981). Isolation and purification of cyanobacteria: some general principles. *The Prokaryotes*. (Ed. by M.P. Starr, H. Stolp, H.G. Truper, A. Balows, Hans G. Schlegel), pp. 212–20. Springer-Verlag, Berlin.

Siebert, J. & Hirsch, P. (1988). Characterization of 15 selected coccal bacteria isolated from Antarctic rock and soil samples from the McMurdo-Dry Valleys (South Victoria Land). *Polar Biology*, **9**, 37–44.

Tschermak-Woess, E. & Friedmann, E.I. (1984). *Hemichloris antarctica*, gen. et spec. nov. (Chlorococcales, Chlorophyta), a cryptoendolithic alga from Antarctica. *Phycologia* **23**, 443–54.

Tuovila, B.J. & LaRock, P.A. (1987). Occurrence and preservation of ATP in Antarctic rocks and its implications in biomass determinations. *Geomicrobiology Journal*, **5**, 105–18.

Vestal, J.R. (1988a). Biomass of the cryptoendolithic microbiota from the Antarctic desert. *Applied and Environmental Microbiology*, **54**, 957–9.

Vestal, J.R. (1988b). Carbon metabolism of the cryptoendolithic microbiota from the Antarctic desert. *Applied and Environmental Microbiology*, **54**, 960–5.

Vestal, J.R. (1989). Primary production of the cryptoendolithic microbiota from the Antarctic desert. *Polarforschung*, **58**, 193–8.

Vestal, J.R. & White, D.C. (1989). Lipid analysis in microbial ecology. *Bioscience*, **39**, 535–41.

Vincent, W.F. (1988). *Microbial Ecosystems of Antarctica*. Cambridge University Press, Cambridge.

Vincent, W.F. & Ellis-Evans, J.C. (eds) (1989). *High Latitude Limnology*. Kluwer, Dordrecht, The Netherlands.

Vishniac, H.S. (1985a). *Cryptococcus friedmannii* a new species of yeast from Antarctica. *Mycologia*, **77**, 149–53.

Weed, R. (1985). *Chronology of chemical and biological weathering of cold desert sandstones in the Dry Valleys, Antarctica*. MS thesis. Department of Geology, University of Maine.

White, D.C. (1983). Analysis of microorganisms in terms of quantity and activity in natural environments. *Microbes in their Natural Environments*. (Ed. by J.H. Slater, R. Whittenbury & J.W.I. Wimpenny), pp. 37–66. Cambridge University Press, Cambridge.

Whittaker, R.H. (1975). *Communities and Ecosystems*, 2nd Edn. Macmillan, New York.

Wynn-Williams, D.D. (1990). Ecological aspects of Antarctic microbiology. *Advances in Microbial Ecology* (Ed. by K.C. Marshall), Vol. 11, pp. 71–146. Plenum Press, New York.